Zootaxa 3957 (1): 037–048
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3957.1.2
http://zoobank.org/urn:lsid:zoobank.org:pub:FCF72565-AF25-45AC-8608-9A0C4D312FFD

Discovery of living Potamolepidae (Porifera: Spongillina) from Nearctic freshwater with description of a new genus

JOHN COPELAND[1], ROBERTO PRONZATO[2] & RENATA MANCONI[3]

[1] *Department of Biology, Lincoln Memorial University, Cumberland Gap Parkway, Harrogate, Tennessee 37752, USA.*
E-mail: john.copeland@lmunet.edu

[2] *Dipartimento di Scienze della Terra, dell'Ambiente e della Vita, Università di Genova, Corso Europa 26, 16132 Genova, Italy.*
E-mail: pronzato@dipteris.unige.it

[3] *Dipartimento di Scienze della Natura e del Territorio, Università di Sassari, Via Muroni 25, 07100 Sassari, Italy.*
E-mail: r.manconi@uniss.it

Abstract

We report here the first record of a living Potamolepidae (*Cherokeesia* n. gen.) from the Nearctic Region and from the northern hemisphere. The new species *Cherokeesia armata* from southern Appalachians diverges at generic and specific level from all the other known taxa of the family Potamolepidae in its unique combination of diagnostic traits: gemmular theca armed by gemmuloscleres ranging from small strongyle-like spicules to stout, large oxeas; absence of pneumatic layer; spiny oxeas as main skeleton megascleres; irregular, slender pauci- to uni-spicular skeletal network. The most similar species belong to the genera *Potamophloios* and *Oncosclera*. The circumtropical biogeographic pattern of extant Potamolepidae, previously considered of Gondwanian to Gondwanian-like origin, is enlarged to the Nearctic. The present Tennessee discovery confirms a wider range of the family. An updated species inventory of Nearctic Spongillina, a checklist of the family Potamolepidae at the global level together with a key to the genera of Potamolepidae are also provided.

Key words: Biodiversity, USA, Appalachians, Tennessee hydrographic basin, sponges, morphology, SEM, taxonomy, biogeography, *Cherokeesia armata* **n. sp.**

Introduction

The importance of freshwater biodiversity cannot be overstated. Freshwater organisms account for almost 6% of all described species, even though freshwater accounts for only 0.01% of the World's water and approximately 0.8% of the Earth's surface (Dudgeon *et al*. 2005).

Due to Pleistocene glaciation, topography, and climate, the southern Appalachian Mountains (East South Central USA) are one of the most biologically diverse regions in the temperate world. High aquatic species diversity has led to this region being recognized as a global center of aquatic biodiversity (McLarney 1999; Curtin *et al*. 2002). Tennessee is considered to be one of the most biologically diverse inland states of the United States (Stein 2002). According to Etnier & Starnes (1993), Tennessee's aquatic fauna diversity is due to the state's geologic and hydrographic diversity.

Six physiographic provinces and five major river drainages are found within Tennessee. The eastern headwater tributaries of the Tennessee River are recognized for their aquatic diversity, and one of these, the Clinch River, is considered a critical watershed for protecting freshwater diversity (Master *et al*. 1998). However, freshwater sponges from Tennessee and the southern Appalachians are poorly known and scarcely documented. The only reports concerning freshwater sponges of Tennessee are those of Hoff (1943) and Parchment (1966). Hoff (1943) documented four species from the Reelfoot Lake region of Tennessee: *Eunapius fragilis* (Leidy, 1851), *Heteromeyenia tubisperma* (Potts, 1881), *Racekiela ryderi* (Potts, 1882), and *Radiospongilla crateriformis* (Potts, 1882). Parchment (1966) recorded *Spongilla lacustris* (Linnaeus, 1759) from Stone River.

Selected Tennessee rivers and streams were surveyed for sponges during June, July and August of 2013 and

Accepted by J. Hooper: 22 Apr. 2015; published: 13 May 2015

2014. Eastern Tennessee waters were surveyed in 2013 and those of middle and western Tennessee in 2014. During the course of the 2013 survey a sponge species was discovered which was morphologically unique from all other known extant freshwater sponges of the Nearctic Biogeographical Realm. These sponges were found within the Nolichucky and Hiwassee Rivers. These rivers arise in the Blue Ridge province and are eastern headwater tributaries of the Tennessee River. The Nolichucky River was revisited on 2 July 2014 and the Hiwassee on 7 July 2014 to collect additional specimens of this sponge.

We report here the first record from the Nearctic Region of a living Potamolepidae and the discovery of a new genus *Cherokeesia* with the description of the type species. The family Potamolepidae was until now considered exclusively from tropical areas of the Neotropical, Afrotropical, Australian, Oriental and Pacific Island biogeographic regions. An updated species inventory of Nearctic Spongillina (Table 1), a checklist of the family Potamolepidae at the global level (Table 2) together with a key to the genera of Potamolepidae (Appendix 1) are also provided.

TABLE 1. Spongillina from freshwater of the Nearctic Region. Updated inventory of extant species.

Cherokeesia armata Copeland, Pronzato and Manconi, 2015; *Corvomeyenia carolinensis* Harrison, 1971; *Corvomeyenia everetti* (Mills, 1884); *Anheteromeyenia argyrosperma* (Potts, 1880); *Corvospongilla becki* Poirrier, 1978; *Corvospongilla novaeterrae* (Potts, 1886); *Dosilia palmeri* (Potts, 1885b); *Dosilia radiospiculata* (Mills, 1888); *Duosclera mackayi* (Carter, 1885); *Ephydatia fluviatilis* (Linnaeus, 1759); *Ephydatia millsi* (Potts, 1887); *Ephydatia muelleri* (Lieberkühn, 1856); *Ephydatia subtilis* Weltner, 1895; *Eunapius fragilis* (Leidy, 1851); *Heteromeyenia baileyi* (Bowerbank, 1863); *Heteromeyenia latitenta* (Potts, 1881); *Heteromeyenia longistylis* Mills, 1884; *Heteromeyenia tentasperma* (Potts, 1880); *Heteromeyenia tubisperma* (Potts, 1881); *Pottsiela aspinosa* (Potts, 1880); *Racekiela biceps* (Lindenschmidt, 1950); *Racekiela ryderi* (Potts, 1882); *Radiospongilla cerebellata* (Bowerbank, 1863); *Radiospongilla crateriformis* (Potts, 1882); *Spongilla alba* Carter, 1849; *Spongilla cenota* Penney and Racek, 1968; *Spongilla lacustris* (Linnaeus, 1759); *Spongilla wagneri* Potts, 1889; *Stratospongilla penneyi* (Harrison, 1979); *Trochospongilla horrida* (Weltner, 1893); *Trochospongilla leidyi* (Bowerbank, 1863); *Trochospongilla pennsylvanica* (Potts, 1882)

Material and methods

Sponges were collected by viewing appropriate substrates while wading. A total of 14 specimens were collected from the Nolichucky River and 12 from the Hiwassee River during 2013 and 2014. Sponges were viewed using a head-loop10 X magnifier for the presence of gemmules. If gemmules were found a section of the sponge was collected. Sponges were preserved in 70% ethanol until processed for Light and Scanning Electron Microscopy (SEM) microscopy

A set of macro- and micro-morphological diagnostic characters considered for identification at the generic and specific levels is focused on growth form, consistency, colour, surface traits, topographic distribution of inhalant and exhalant apertures, architecture of ectosomal and choanosomal skeleton, topographic distribution and traits of skeletal megascleres, microscleres, and gemmules, gemmular architecture (gemmular cage, foramen, gemmular theca, architecture of pneumatic layer and spatial arrangement of spicules), and gemmuloscleres morphology (Manconi & Pronzato, 2002). The nomenclature of diagnostic morphotraits follows Manconi & Pronzato (2002 p. 923–924).

To characterize morphotraits, representative fragments of sponges were dissected for Light Microscopy (LM) and/or SEM observation. To obtain perfectly cleaned spicule preparations for SEM observation and LM slides for a voucher collection, sponge fragments were dissolved in boiling 65% nitric acid in test tubes and then suspended in water. To achieve total sedimentation of the lighter, smaller spicules, dissociated spicules were suspended and repeatedly rinsed with distilled water and then dehydrated in graded ethanol series with a gap of 15–20 minutes between successive washing (Manconi & Pronzato, 2000). Alcohol (95%) was poured from tubes with a slow movement to leave the deposit of spicules in 0.5 ml of the medium in the tube before dropping some suspended spicules on slides for LM and SEM analysis (Manconi & Pronzato, 2000). The presence of a glass substratum under the spicules gives the best results as a perfectly black background in the SEM photographs. Dry body fragments, dissociated spicules, entire gemmules, and their cross-sections were sputter-coated with gold and observed by SEM (Leo 982). Morphometries of diagnostic traits were performed by LM and/or SEM. To

characterize the spicular complement of the new species, 50–90 spicules for each diagnostic spicular type (megascleres and gemmuloscleres) were measured.

Holotype and paratypes were registered at the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM), and one paratype at the Dipartimento di Scienze della Terra, dell'Ambiente e della Vita, Università di Genova (DTRG), Italy. Representative specimens were compared to original descriptions and materials from historical collections. Acronyms: BMNH (The Natural History Museum, London, United Kingdom), MNHN (Muséum National d'Histoire Naturelle, Paris, France), MNRJ Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil, MRAC (Musée Royal de l'Afrique Centrale de Tervuren KMMA, Belgium), ZMB (Zoologisches Museum für Naturkunde an der Universität Humboldt, Berlin, Germany).

Systematic Accounts

PHYLUM PORIFERA GRANT, 1836

CLASS DEMOSPONGIAE SOLLAS, 1885

ORDER HAPLOSCLERIDA TOPSENT, 1928

SUBORDER SPONGILLINA MANCONI and PRONZATO, 2002

FAMILY POTAMOLEPIDAE BRIEN, 1967

Synonymy. Potamolepidae Brien, 1967; Manconi and Pronzato, 2002; Potamophloiinae Brien, 1969
[Type genus *Potamolepis* Marshall, 1883]

Family definition (emended from Manconi & Pronzato, 2002, 2009). Spongillina with growth form from encrusting or massive to arborescent with irregular lobes, ridges or branches. Consistency from rigid to stony hard, fragile particularly at the sponge base that generally remains adherent to substrata during sampling. Spongin scanty except for the basal spongin plate and gemmular theca. Surface smooth to irregular with chimneys, to conulose with apices of ascending primary fibers supporting conules. Oscules with exhalant star-shaped canals in some cases. No special ectosomal skeleton except for spicular tufts supporting conules and tangential microscleres in the dermal membrane (only some genera). Choanosomal skeleton irregularly alveolate-reticulate with mono- to pauci-spicular tracts sometimes ascending towards the surface, skeletal network notably dense at the surface and more loose and irregular at the sponge base. Megascleres strongyles to oxeas from smooth to ornamented by variably dense granules/spines/tubercles. Microscleres, if present, slender oxeas. Gemmules, when present, single to grouped, sometimes free at the sponge base or more frequently sessile and strictly adhering to the substratum by the basal spongin plate. Gemmular theca mono-, bi- to tri-layered, usually of compact spongin, with more or less tangentially embedded gemmuloscleres. Pneumatic layer absent to scarcely developed of fibrous, not chambered spongin. Foramen not always evident. Gemmuloscleres strongyle-like, short to elongate, ovular to variably bent (C-like to button-like) variably ornamented to entirely smooth. A second category of gemmuloscleres as large, stout, spiny to smooth oxeas. Parenchymella larvae entirely ciliated, with spicules.

Genus *Cherokeesia* n. gen.

Diagnosis. *Cherokeesia* diverges from all the other known genera of the family Potamolepidae for diagnostic traits of the gemmules and skeleton. See species diagnosis.

Etymology. The genus name (feminine) is derived from the valiant and proud North American native people known as the Cherokee (possibly from the *Choctaw Cha-la-kee* meaning "people of the mountains" or *Chi-luk-ik-bi* meaning "people of the cave country").

***Cherokeesia armata* n. sp.**
[Type species] (Figs 1–4; Tabs 1–2; Appendix 1)

Holotype. USNM 1264992, type locality Nolichucky River (36°09′22″ N, 82°43′27.5″ W) an eastern headwater tributary of the Tennessee River, USA, Tennessee, Blue Ridge Province, J. Copeland leg., 2, July 2014. **Paratypes**. USNM 1264993–1265000, Nolichucky River (36°09′22″ N, 82°43′27.5″ W) an eastern headwater tributary of the Tennessee River, USA, Tennessee, Blue Ridge Province, J. Copeland leg., 2, July 2014; USNM 1266150, Nolichucky River (36° 09′ 22″ N, 82° 43′ 27.5″ W) an eastern headwater tributary of the Tennessee River, USA, Blue Ridge Province, J. Copeland leg. 26 June 2013 on 1 slide; USNM 1266148, ibid., on 2 slides; USNM 1266151, ibid., on 2 slides; USNM 1266149, Nolichucky River (36° 10′ 54.1″ N, 82° 31′ 45.4″ W) an eastern headwater tributary of the Tennessee River, USA, Tennessee, Blue Ridge Province, J. Copeland leg., 29 July 2013 on 1 slide; USNM 1266145, Hiwassee River (35° 13′ 13.6″ N, 84° 31′ 07.1″ W), an eastern headwater tributary of the Tennessee River, USA, Tennessee, Blue Ridge Province, J. Copeland leg., 26 July 2013 on 2 slides; USNM 1266146, ibid., on 2 slides; USNM 1266147, ibid., on 2 slides. DTRG FW 763 specimen fragment is from Nolichucky River (36° 10′ 54.1″ N, 82° 31′ 45.4″ W) collected 29 July 2013 (Fig. 1).

FIGURE 1. Global biogeographic distribution of family Potamolepidae with inserts showing the distribution of *Cherokeesia* n. gen. within Tennessee and location of Tennessee within the United States. Approximate location of Tennessee is indicated by asterix. Fossils are indicated by plus symbol .

Comparative material. *Echinospongilla brichardi* (Brien, 1974) holotype MRAC 1430, leg. M. Brichard, v.1973, Urundi, Lake Tanganyika, Usumbura. *Potamolepis stendelli* Jaffe, 1916 holotype MRAC 410-411, Kasenga, Lake Luapula, on shell fragments, mission Stappers, 25.vii.1911, 0–10 m depth, by dredge. *Oncosclera jewelli* (Volkmer, 1963) holotype MNRJ 001, Rio Thainas, São Francisco da Paula, Rio Grande do Sul, 10.ix.1960, det. C. Volkmer-Ribeiro. *Oncosclera asiatica* Manconi and Ruengsawang, 2012**,** holotype MSNG 56534a, Pong River**,** Thailand; *Sterrastrolepis brasiliensis* Volkmer-Ribeiro and De Rosa Barbosa, 1978 holotype MNRJ 092 (ex-MCN 113), 3 gemmules, Turvo River, branch of Paranaiba River, Paranà Basin, Goias State, Brazil. *Uruguaya corallioides* (Bowerbank, 1863) BMNH 1952.6.30.2, Uruguay River. MNHN DX325, Orinoco River, 1885, M. Chaffangeon. ZMB 1703, Amazonia, ii.1892, V. Honnef.

Diagnosis. This species can be distinguished by the unique combination of morphotraits. A distinctive trait is the spicular complement of the gemmular theca. Gemmular theca strongly armed by gemmuloscleres of two

categories: large, stout, spiny to smooth oxeas (megascleres size) intermingled with smooth strongyles (C-like to bean-like), both tangentially embedded in the entire thickness of the theca. Pneumatic layer absent.

Etymology. The specific epithet *armata* refers to the gemmular theca strongly armed by gemmuloscleres of two categories.

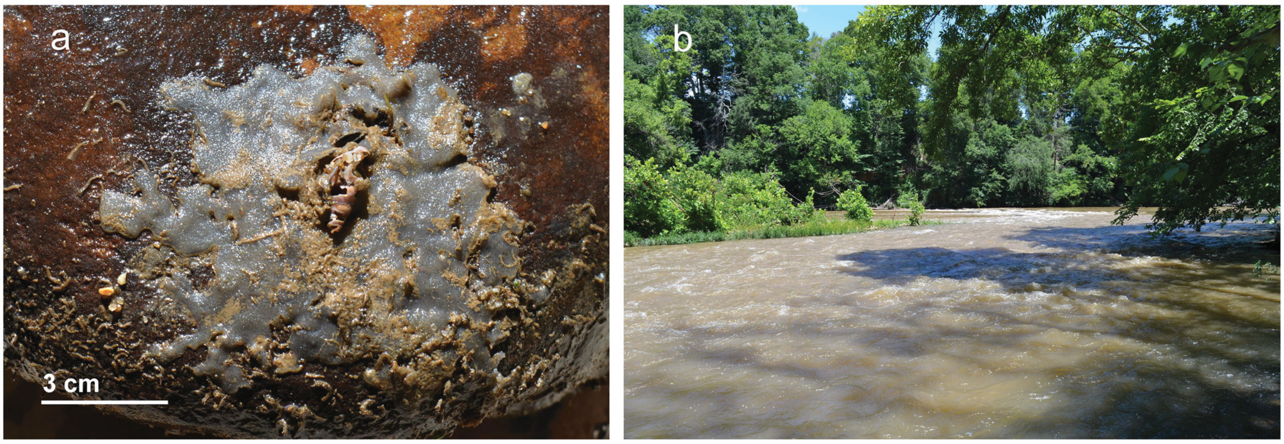

FIGURE. 2. *Cherokeesia armata* **n. sp. a**, Holotype *in vivo* encrusting a rock. **b**, type locality from the Nolichucky River in the Tennessee hydrographic basin.

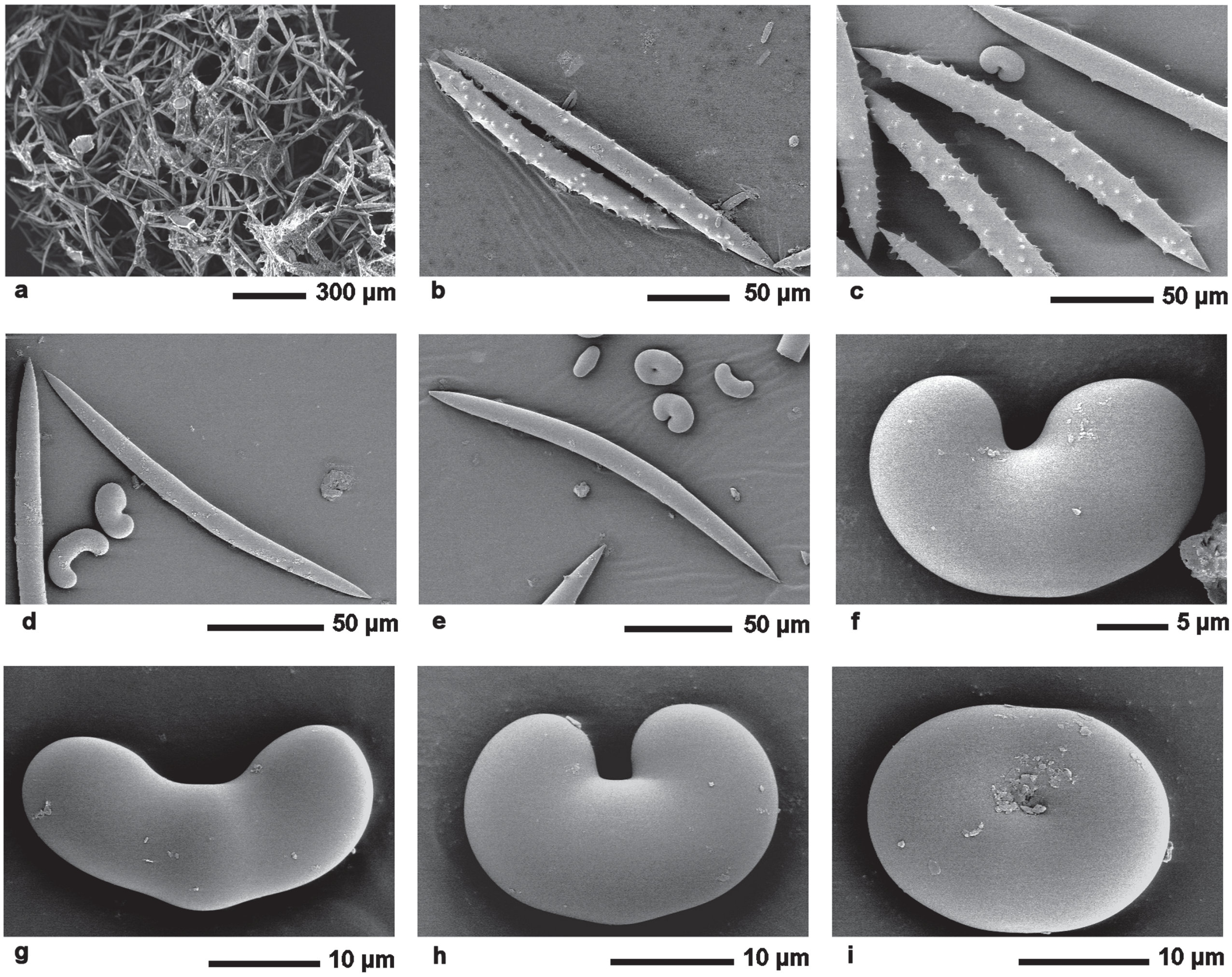

FIGURE. 3. *Cherokeesia armata* **n. sp.** Skeleton and spicular complement of type material series from the Nolichucky and Hiwassee rivers. **a,** Skeletal network of megascleres. **b–i,** Megascleres as spiny oxeas and gemmuloscleres spiny to smooth oxeas and C- to bean-like or ovoid strongyles; see also Fig. 5.

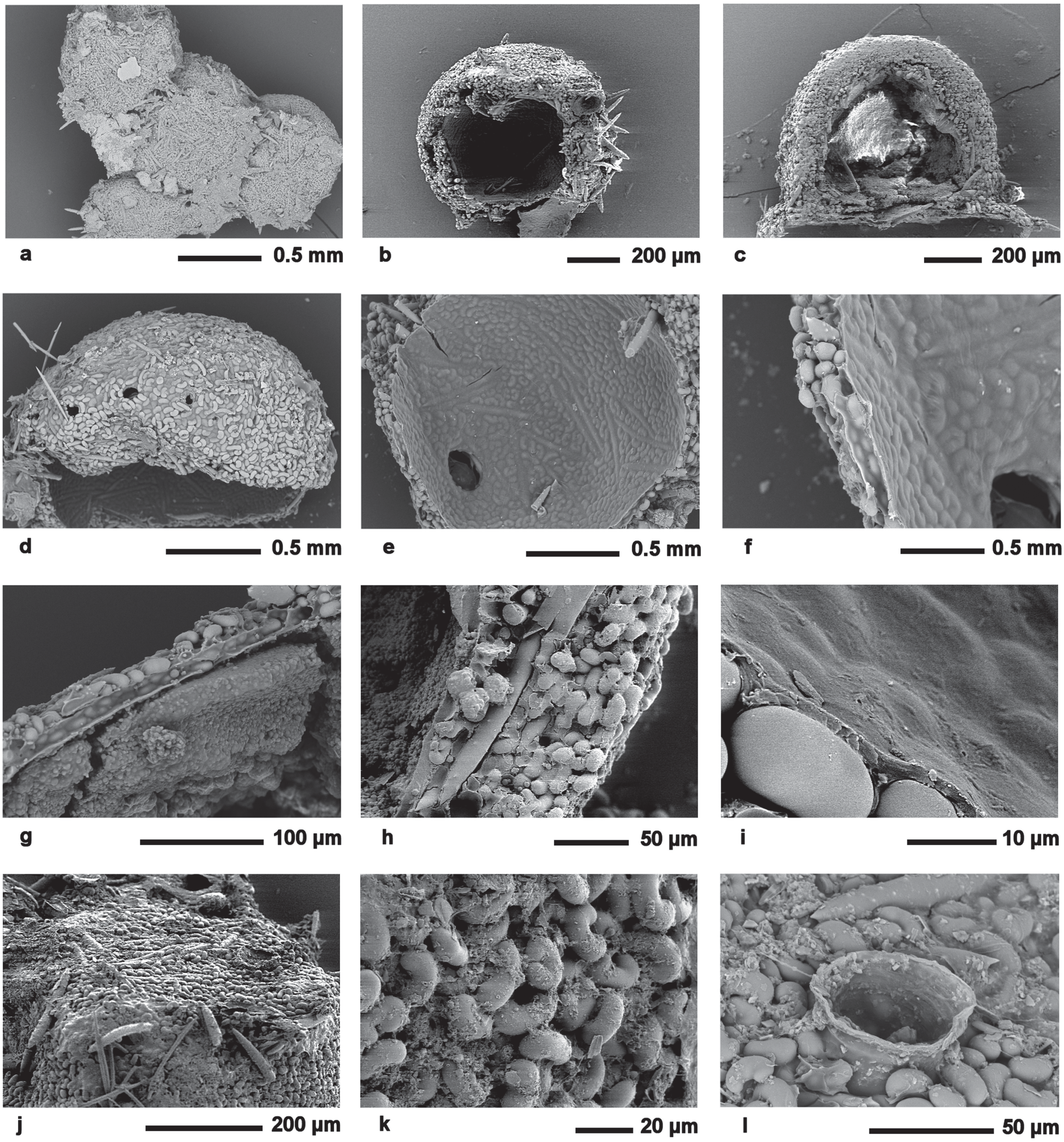

FIGURE. 4. *Cherokeesia armata* **n. sp.** Gemmular traits of type material series from the Nolichucky and Hiwassee rivers. **a–l,** Gemmule architecture and traits of the gemmular theca. **A,** Gemmules in a cluster. **b–c,** Gemmular theca (cross section). **d,** Gemmular surface with multiforamina, and gemmuloscleres strongyle-like in a mosaic. Foramen apertures with simple collar. **e,** Inner surface of gemmular theca with foraminal aperture and evident outlines of two categories of gemmuloscleres, strongyle-like and large spiny oxeas. **f**, Gemmular theca with thin wall of a few layers of gemmuloscleres; inner view of foraminal aperture on the right (detail of cross section). **g**, Gemmular theca with a mass of staminal cells (cross section). **h**, Magnification of the tri-layered gemmular theca of compact spongin armed by two categories of embedded spicules as small, smooth strongyles and large, stout, spiny oxeas (cross section). **i**, Inner layer of the theca (compact spongin) and gemmuloscleres (smooth, short strongyles) strictly adhering to each other by spongin. **j,** Gemmular surface. **k,** Small, smooth strongyles at the outer layer of the theca. **l,** Gemmular surface with single foraminal aperture and gemmuloscleres surrounding the basal portion of the short, simple collar.

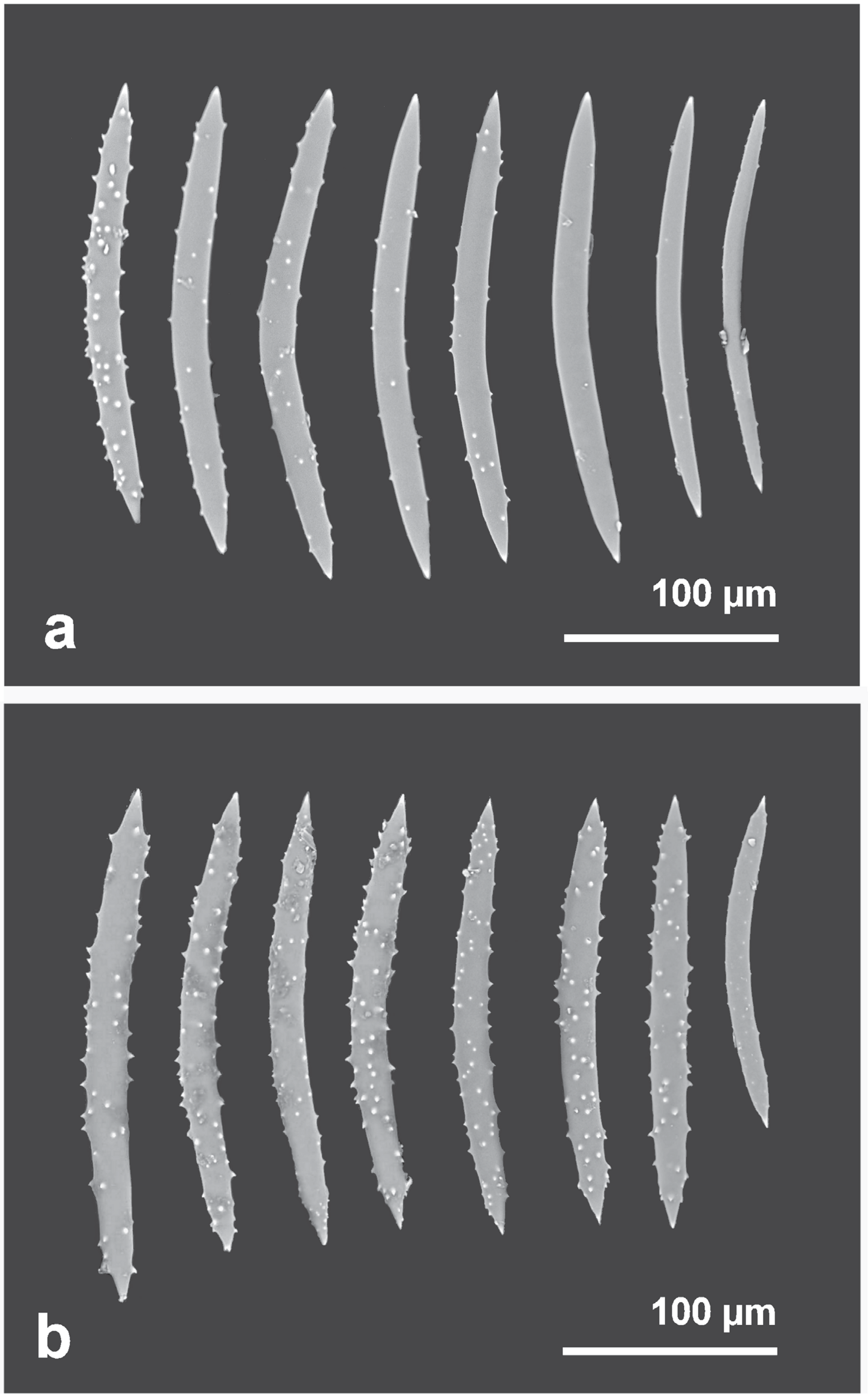

FIGURE 5. *Cherokeesia armata* **n. sp. a**, gemmuloscleres type I as large acanthoxeas from notably spiny to almost smooth; **b**, megascleres of the skeleton as stout acanthoxeas.

Description. Growth form encrusting as minute cushions, 1–4 mm in thickness, largest specimen 10 cm in diameter (Fig. 2a). **Consistency** hard, fragile *in vivo*. **Colour** light gray *in vivo*, somewhat transparent; white (in alcohol). **Surfac**e alveolate with slight hispidation of more or less erected ectosomal spicules supporting small scattered conules. **Oscules** conspicuous *in vivo*, numerous, scattered. **Inhalant apertures** scattered. **Ectosomal skeleton** irregularly alveolate as a mesh network of mono- to pauci-spicular tracts (oxeas) supporting the dermal membrane. **Choanosomal skeleton** irregularly alveolate network, with mono-spicular polygonal meshes (100–200 µm in diameter) and few, scarcely developed, ascending pauci-spicular tracts. **Spongin** notably scanty, except for the gemmular theca and the basal spongin plate. **Basal spongin plate** well developed, and adhering to the flat base of gemmules. **Megascleres** stout, spiny oxeas 161.8 to 228 (199.5 ± 15.8) x 12.3 to 20.7 (16.6 ± 1.9) µm (standard error of the mean length = 2.2; standard error of the mean width = 0.3) with gradually pointed to abruptly pointed tips, straight to slightly bent; spines straight to recurving towards the spicule tips (Figs 3a–e, 5b). **Microscleres** absent. **Gemmules** sessile, at the sponge base, hemispherical (up to 800 µm in diameter), flat at the base (Fig. 4a–b) strictly adhering to the substrate by the basal spongin plate; single or in small clusters of 3–4 gemmules; strongly armed by tangential gemmuloscleres of two categories. **Foramen** single to multiforamina (up to 3) (Fig. 4d–f) with simple collar (Fig. 4l) (20–40 µm in diameter) sometimes closed by a spongin lamina. **Gemmular theca** of compact spongin variably thick (25–150 µm in thickness)**,** tri-layered, with gemmuloscleres (up to 10 layers) of two categories intermingled and tangentially embedded (Fig. 4f–g). **Outer layer** of thin compact spongin, like a film on gemmuloscleres surfaces (Fig. 4j–k). **Middle layer** of a thin non-alveolate layer of compact spongin (pneumatic layer absent). **Inner layer** of compact spongin (Fig. 4e–f and i). **Gemmuloscleres** of two types (strongyle-like spicules and spiny to smooth oxeas). **Type I**. Dominant, in several layers (5–7) more or less in a mosaic-manner, joined by a conspicuous amount of compact spongin. Strongyle-like spicules 29.3 to 17.0 (22.4 ± 2.5) x 17.1 to 8.5 (10.3 ± 1.3) µm (standard deviation of the mean length = 0.3; standard error of the mean width = 0.1), stout, entirely smooth, from extremely bent C-shaped to bean-shaped up to ring-shaped or button-like (Fig. 3f–i). Rare, elongate, short typical strongyles, slightly bent to straight (50–100 x 10 µm) also present. **Type II**. Less abundant, large, stout, spiny to smooth oxeas tangentially embedded intermingled with gemmuloscleres type I in the entire thickness of the theca (Figs 4h, 5a). Oxeas (173.3 to 258 (219.7 ± 16.7) x 9.8 to 17.4 (14.7 ± 1.9) µm, (standard error of length = 16.7; standard error of mean width = 0.3) abruptly pointed, spiny to smooth, with acute spines straight to recurved toward the tips.

Habitat. On the underside of submerged hand size rocks to small boulders in flowing water at depths ranging from 20 to 200 cm. Gemmules were recorded only in some specimens collected during summertime.

Geographic distribution. Currently known only from the Nolichucky (Fig. 1) and Hiwassee Rivers (Blue Ridge Province, Southern Appalachians) in the Tennessee River hydrographic basin.

Discussion

Cherokeesia armata has a unique combination of diagnostic traits: gemmular theca armed by strongyle-like gemmuloscleres intermingled with stout, large oxeas; absence of pneumatic layer; spiny oxeas as skeletal megascleres; irregular, light pauci- to uni-spicular skeletal network. Thereby *C. armata* diverges at the generic level from all other taxa of the family Potamolepidae. A key to the genera of Potamolepidae is presented in Appendix 1.

The most similar species belong to the genera *Oncosclera* and *Potamophloios*.

As in *Oncosclera* the skeletal megascleres of *Cherokeesia* are oxeas, but in the former oxeas are smooth while in the latter oxeas are spiny. As for the gemmular spicules, *Oncosclera* bears gemmuloscleres highly variable from true strongyles to irregularly ovoid strongyles, from smooth to curved with short spines and tubercles vs. *Cherokeesia* bearing gemmuloscleres very short and strongly curved, smooth strongyles and large spiny to smooth oxeas.

As in *Potamophloios* gemmuloscleres type I of *Cherokeesia* are from elongate to ovular, smooth strongyles tangentially embedded in the gemmular theca. Moreover the theca of the new genus embeds large spiny to smooth oxeas. In *Potamophloios* megascleres are smooth, slightly bent strongyles with inflated tips vs. the spiny oxeas (megascleres) of *Cherokeesia*.

TABLE 2. Checklist of the family Potamolepidae at global level. Zoogeographic regions indicated by AT-NA-NT-PA-PAC referring respectively to the Afrotropical, Nearctic, Neotropical, Palearctic, and Pacific Islands realms. Fossil records indicated by †.

Family POTAMOLEPIDAE Brien, 1967 (7 genera, 33 species) AT-NA-NT-PA-PAC
Cherokeesia Copeland, Pronzato and Manconi, 2015 (**1 species**) NA
C. armata Copeland, Pronzato and Manconi, 2015 (R. Tennessee, USA) monotypic N
Echinospongilla Manconi and Pronzato, 2002 (**1 species**) AT
E. brichardi (Brien, 1974) (L. Tanganyika) monotypic AT
Oncosclera Volkmer-Ribeiro, 1970 (**17 species**) AT-NT-OL-PA-PAC
O. asiatica Manconi and Ruengsawang, 2012 (Mekong basin,Thailand) OL
O. atrata (Bonetto and Ezcurra de Drago, 1970) (R. Apurà, Argentina) NT
O. diahoti (Rützler, 1968) (New Caledonia) PAC
O. gilsoni (Topsent, 1912) (Fiji) PAC
O. intermedia (Bonetto and Ezcurra de Drago, 1973) (R. Orinoco, Venezuela, Brazil) NT
O. jewelli (Volkmer-Ribeiro, 1963) (Rio Grande do Sul, Brazil) type species NT
O. kaniensis† Matsuoka and Masuda, 2000 (Japan, Miocene) PA†
O. macrospiculata (Stephens, 1919) (Western Africa) AT
O. navicella (Carter, 1881) (Brazil, Argentina, Uruguay, Venezuela) NT
O. petricola (Bonetto and Ezcurra de Drago, 1967) (R. Uruguay, Argentina, Brazil) NT
O. ponsi (Bonetto and Ezcurra de Drago, 1968) (R. Uruguay, Argentina) NT
O. rousseleti (Kirkpatrick, 1906) (R. Zambezi, Africa) AT
O. schubarti (Bonetto and Ezcurra de Drago, 1967) (R. Uruguay, Argentina, Brazil) NT
O. schubotzi (Weltner, 1913) (Aruwimi, Congo basin) AT
O. spinifera (Bonetto and Ezcurra de Drago, 1973) (R. Orinoco, Venezuela, Brazil) NT
O. stolonifera (Bonetto and Ezcurra de Drago, 1967) (R. Pirù, Argentina) NT
O. tonollii (Bonetto and Ezcurra de Drago, 1968) (R. Uruguay, Argentina, Parami, Brazil) NT
Potamolepis Marshall, 1883 (**7 specie**s) AT
P. belingana Lévi, 1965 (Cameroon, R. Ivindo Gabon) AT
P. chartaria Marshall, 1883 (Isangila, Congo basin, R. Luapula, L. Tanganyika, R. Niger) AT
P. leubnitziae Marshall, 1883 (Congo basin, L. Mweru, R. Niger, L. Tanganyika) type species AT
P. marshalli Burton, 1938 (Matadi Congo basin) AT
P. micropora Burton, 1938 (Matadi-Congo basin) AT
P. pechueli Marshall, 1883 (Matadi-Matemba Congo basin, L. Tanganyika) AT
P. weltneri Moore, 1903 (L. Tanganyika, Zimbabwe) AT
Potamophloios Brien, 1970 (**6 species**) AT-NA-NT
Potamophloios canadensis† Pisera, Siver and Wolf, 2013 (northern Canada, Middle Eocene) NA
P. gilberti Brien, 1969 (L. Mweru, R. Luapula) AT
P. guairensis Volkmer-Ribeiro, Parolin, Fürstenau-Oliveira, Menezes, 2010 (L. Itaipu, Brazil) NT
P. hispida Brien, 1969 (L. Mweru, R. Luapula) AT
P. songoloensis Brien, 1969 (L. Mweru, R. Luapula) AT
P. stendelli (Jaffé, 1916) (L. Mweru, L. Luapula, L. Tanganyika) type species AT
P. symoensi (Brien, 1967) (Luapula basin) AT
Sterrastrolepis Volkmer-Ribeiro and De Rosa Barbosa, 1978 (**1 species**) NT
S. brasiliensis Volkmer-Ribeiro and De Rosa Barbosa, 1978 (R. Turvo, Brazil) monotypic NT
Uruguaya Carter, 1881 (**1 species**) NT
U. corallioides (Bowerbank, 1863) (Brazil, Uruguay, Venezuela, Paraguay) monotypic NT

Finally the skeleton of *Cherokeesia* is slender, irregular, alveolate network, with mono-spicular polygonal meshes and few, scarcely developed, pauci-spicular tracts. In contrast *Potamophloios* and *Oncosclera* display a skeleton evidently stout and never mono-spicular.

Cherokeesia armata represents the first record of a living potamolepid species from the Nearctic and, more in general, from the northern hemisphere. This record increases the taxonomic richness of the Nearctic Region harbouring, at present, three families, 15 genera, and 33 species (Table 1) (Manconi & Pronzato 2002, 2007, 2008, 2009, 2015; van Soest *et al*. 2014). Endemicity is high (>50 %) with 16 taxa endemic at species level.

The Tennessee record of *C. armata* represents an intriguing puzzle difficult to explain from a biogeographic point of view. As it is known the geographical distribution of Spongillina is related to geological and climatic vicissitudes of the continents, to the long-term dynamics of hydrographic basins, and to sponge dispersal power (Pronzato *et al*. 1993; Pronzato & Manconi 1994; Manconi & Pronzato 2007, 2015). The main environmental constraint for large scale spreading, i.e. among continental plates seems to be due to oceans. At a lesser scale spreading of sponges within continental waters is constrained by natural habitat fragmentation (ponds, lakes, courses, springs, coastal basins, ephemeral basins, and reservoirs). Swimming larvae disperse exclusively downstream by running water and flooding. In contrast, the dispersal power by gemmules is apparently higher and favored by a successful trend in gemmule morpho-functional adaptive radiation (e.g., gemmular theca architecture, spiny spicules, and physiology of cryptobiosis by gemmular staminal cells). Gemmules are the key structure for freshwater sponge dispersal (Manconi & Pronzato 2007). Gemmules provide a potentially efficient dispersal structure and cryptobiosis is a successful adaptive strategy to perform *in situ* both survival and persistence of sponge populations (Manconi & Pronzato 2008, 2015; Pronzato & Manconi 1995).

Spongillina species belonging to families that do not produce gemmules (Lubomirskiidae) are confined in very restricted areas; on the contrary the species belonging to the widespread families, i.e. Spongillidae and Metaniidae display high performance gemmules in dispersal terms (light free gemmules, spiny gemmuloscleres, and pneumatic layer) (Manconi & Pronzato 2004, 2007, 2015). The functional role of "heavy, sessile gemmules strictly adhering to the substratum" produced by *Cherokeesia*, and most Potamolepidae, seems to be *in situ* long-term persistence, and putatively local downstream dispersal by gemmules settled on hard driftable substrata.

The poor adaptation of potamolepid gemmules to overland dispersal matches well the status of species endemic to ancient hydrographic basins in a Neotropical and Afrotropical range (Fig. 1), although this trait does not explain records in Australian (New Caledonia) and Pacific Oceanic Islands Regions (Fiji). The disjunct geographic range of the family appeared to be the result of the Gondwanian splitting as first proposed by Bonetto & Ezcurra de Drago (1967) and supported by other authors (Brien 1970ab; Volkmer-Ribeiro 1990; Manconi & Pronzato 2002). The records of an eastern Palaearctic fossil by Matsuoka & Masuda (2000) and a record of a living species in the Oriental Region induced Manconi *et al*. (2012, 2013) to consider the biogeographic pattern of Potamolepidae as Gondwanian-like until further palaeontological data or new findings of recent species will clarify better the historical biogeography of the family. A new fossil potamolepid was recently recorded by Pisera *et al*. (2013) in a palaeotropical basin of Canada. The zoogeographic distribution of the family Potamolepidae is presented in Table 2.

The apparently aberrant record of the present new genus/species in Tennessee (see Manconi & Pronzato 2005, 2007, 2015) corroborates the palaeodata for Potamolepidae from the northern hemisphere i.e. *Oncosclera kaniensis* from the Japanese Miocene and *Potamophloios canadensis* from a tropical palaeolake of the North American Middle Eocene. Records of both fossil and extant Potamolepidae do not fit a Gondwanian origin, being continent drift quite similar to the current position during Eocene and Miocene. The hypothesis of a wider distribution of potamolepid sponges in the past is supported.

Acknowledgements

J. Copeland acknowledges Lincoln Memorial University, Tennessee Wildlife Resources Agency, and Well Being Foundation for funding, Stan Kunigelis and Jessee Tussing and Tucker Jett for field and laboratory assistance. R. Manconi acknowledges the Regione Autonoma Sardegna (RAS-CRP-60215-2012), Italian Ministero dell'Istruzione, dell'Università e della Ricerca (MIUR-PRIN), and Fondazione Banco di Sardegna. Also, we gratefully acknowledge the expertise and constructive suggestions of the reviewers of this paper.

References

Bonetto, A.A. & Ezcurra de Drago, I.D. (1973) Aportes al conocimiento de las esponjas del Orinoco. *Physis*, 28 (76), 211–216.

Brien, P. (1970a) Les Potamolepides africaines nouvelles du Luapula et du Lac Moero. Polyphylétisme des éponges d'eau douce. *In* W.G. Academic Press Fry (Eds.), *Biology of the Porifera*. Symposium of the Zoological Society London 25, Academic Press, London, pp. 163–187.

Brien, P. (1970b) Deux éponges du Cameroun: *Corvospongilla boehmii* (Hilgendorf), *Eunapius nitens* (Carter). *Revue de Zoologie et de Botanique africaines*, 81 (1–2), 51–61.

Curtin, M., McCown, D., Morris, E., Shields, C. & Whitley, K. (2002) *Land use and biodiversity on the Highland Plateau: a Carolina Environmental Program Report*. Highlands Biological Station, Highlands, NC. pp. 1–57

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A-H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and onservation challenges. *Biological Reviews*, 81, 163–182.
http://dx.doi.org/10.1017/S1464793105006950

Etnier, D.A. & Starnes, W.C. (1993) *The fishes of Tennessee*. The University of Tennessee Press, Knoxville, TN, 681 pp.

Hoff, C.C. (1943) Some records of sponges, branchiobdellids, and molluscs from the Reelfoot Lake region. *Journal of the Tennessee Academy of Science*, 18, 223–227.

Manconi, R. & Pronzato, R. (2000) Rediscovery of the type material of *Spongilla lacustris* (L., 1759) in the Linnean herbarium. *Italian Journal of Zoology*, 67 (1), 89–92.
http://dx.doi.org/10.1080/11250000009356300

Manconi, R. & Pronzato, R. (2002) Suborder: Spongillina subord. nov.: Freshwater Sponges, *In:* Hooper, J.N.A. & Van Soest, R.W.M (Eds), *Systema Porifera: A Guide to the Classification of Sponges*. Kluwer Academic/Plenum Publishers, New York, pp. 921–1019.

Manconi, R. & Pronzato, R. (2004) Resting stages of *Corvospongilla* sp. from Mesopotamia, Iraq. *In:* Pansini, M., Pronzato, R., Bavestrello, G. & Manconi, R. (Eds.), *Sponge Science in the New Millennium*. Bollettino dei Musei e Istituti Biologici dell'Università di Genova, 68 (2003–2004), pp. 441–448.

Manconi, R. & Pronzato, R. (2005) Freshwater sponges of the West Indies: discovery of Spongillidae (Haplosclerida, Spongillina) from Cuba with biogeographic notes and a checklist for the circum-Caribbean area. *Journal of Natural History*, 39 (36), 3235–3253.
http://dx.doi.org/10.1080/00222930500307327

Manconi, R. & Pronzato, R. (2007) Gemmules as a key structure for the adaptive radiation of freshwater sponges: A morpho-functional and biogeographical study. *In:* Custódio, M.R., Lôbo-Hajdu, G., Hajdu, E. & Muricy, M. (Eds.), *Porifera Research: Biodiversity, Innovation, Sustainability.* Museu Nacional, Serie Livros 28, Rio de Janeiro, pp. 61–77.

Manconi, R. & Pronzato, R. (2008) Global diversity of sponges (Porifera: Spongillina) in freshwater. *Hydrobiologia*, 595, 27–33.
http://dx.doi.org/10.1007/978-1-4020-8259-7_3

Manconi, R. & Pronzato, R. (2009) Atlas of African freshwater sponges. Studies in Afrotropical Zoology, vol. 295. Royal Museum for Central Africa, Tervuren.

Manconi, R. & Pronzato, R. (2015) Phylum Porifera. *In:* Thorp, J. & Rogers, D.C. (Eds.), Ecology and General Biology: Thorp and Covich's Freshwater Invertebrates. Academic Press, pp. 133–157.

Manconi, R., Ruengsawang, N., Ledda, F.D., Hanjavanit, C. & Sangpradub, N. (2012) Biodiversity assessment in the Lower Mekong basin: first record of the genus *Oncosclera* (Porifera: Spongillina: Potamolepidae) from the Oriental Region. *Zootaxa*, 3544, 41–51.

Manconi, R., Ruengsawang, N., Vannachak, V., Hanjavanit, C., Sangpradub, N. & Pronzato, R. (2013) Biodiversity in South East Asia: an overview of freshwater sponges (Porifera: Demospongiae: Spongillina). *Journal of Limnology*, 72 (s2), 313–326.
http://dx.doi.org/10.4081/jlimnol.2013.s2.e15

Matsuoka, T. & Masuda, Y. (2000) A new potamolepid freshwater sponge (Demospongiae) from the Miocene Nakamura Formation, central Japan. *Paleontological Research*, 4 (2), 131–137.

Master, L.L., Flack, S.R. & Stein, B.A. (Eds.), (1998) *Rivers of life: critical watersheds for protecting freshwater biodiversity.* The Nature Conservancy, Arlington, VA, 71 pp.

McLarney, W.O. (Compiler) (1999) *Protection of aquatic biodiversity in the southern Appalachian National Forests and their watersheds: information for use in the forest plan revision process and beyond*. A Report of the Southern Appalachian Forest Coalition and Pacific Rivers Council, 34 pp.

Parchment, J.G. (1966) Notes on the ecology of sponges. *Journal of the Tennessee Academy of Science*, 41, 1–65.

Pisera, A., Siver, P.A. & Wolf, A.P. (2013) A first account of freshwater potamolepid sponges (Demospongiae, Spongillina, Potamolepidae) from the middle Eocene: biogeographic and paleoclimatic implications. *Journal of Paleontology*, 87 (3), 373–378.
http://dx.doi.org/10.1666/12-079.1

Pronzato, R. & Manconi, R. (1994) Adaptive strategies of sponges in inland waters. *Bollettino di Zoologia*, 61, 395–401.
http://dx.doi.org/10.1080/11250009409355912

Pronzato, R. & Manconi, R. (1994) Life history of *Ephydatia fluviatilis*: a model for adaptive strategies in discontinuous habitats. *In:* van Soest, R.W.M., van Kempen, Th.M.G. & Braekman, J.C. (Eds.), *Sponges in time and space*. Rotterdam: Balkema, pp. 327–331.

Pronzato, R. & R. Manconi (1995) Long-term dynamics of a freshwater sponge population. *Freshwater Biology*, 33, 485–495. http://dx.doi.org/10.1111/j.1365-2427.1995.tb00408.x

Pronzato, R., Manconi, R. & Corriero, G. (1993) Biorhythm and environmental control in the life history of *Ephydatia fluviatilis* (Demospongiae, Spongillidae). *Bollettino di Zoologia*, 60, 63–67. http://dx.doi.org/10.1080/11250009309355792

Stein, B.A. (2002) *States of the Union: Ranking America's Biodiversity.* NatureServe, Arlington, VA, USA, 25 pp.

Van Soest R.W.M., Boury-Esnault, N., Hooper, J.N.A., Rützler, K., de Voogd, N.J., Alvarez de Glasby, B., Hajdu, E., Pisera, A.B., Manconi, R., Schoenberg, C., Janussen, D., Tabachnick, K.R., Klautau, M., Picton, B., Kelly, M. & Vacelet, J. (Eds.), (2014) World Porifera Database. Available from: http://www.marinespecies.org/porifera (July 2014)

Volkmer-Ribeiro, C. (1990) A new insight into the systematics, evolution and taxonomy of freshwater sponges. *In:* Rützler, K. (Ed.), *New perspectives in Sponge Biology*. Smithsonian Institution Press, Washington DC, USA, pp. 323–331.

APPENDIX 1. Key to genera of the family Potamolepidae Brien, 1967.

1. Gemmules present, gemmuloscleres strongyle-like forms and oxeas tangentially arranged in the gemmular theca 2
- Gemmules absent 3
2. Microscleres oxeas with granule/tubercles/spines arranged in rosettes; megascleres stout, smooth to granulate strongyles; gemmules sub-spherical; gemmuloscleres, tangentially embedded in the theca, strongyle-like ovoid with partly granulate surface . . . . ***Sterrastrolepis***
- Microscleres absent, gemmuloscleres tangentially embedded in the theca 4
3. Megascleres smooth strongyles; microscleres/gemmules absent . . . . ***Echinospongilla***
- Megascleres of 2 categories, smooth strongyles/oxeas; microscleres/gemmules absent . . . . ***Potamolepis***
4. Megascleres strongyles 5
- Megascleres oxeas. 6
5. Megascleres smooth, stout strongyles with inflated tips; microscleres absent; gemmules present; gemmuloscleres from elongate to ovular smooth strongyles. . . . . ***Potamophloios***
- Megascleres granulate strongyles (skeleton) and stout smooth oxeas (gemmular cage); microscleres absent; gemmules present; gemmuloscleres smooth strongyles (bean-like) . . . . ***Uruguaya***
6. Megascleres smooth, stout oxeas rarely with tubercles/granules; microscleres absent; gemmules present; gemmuloscleres from true strongyles to irregularly ovoid strongyles, smooth to spiny with short spines/tubercles more dense at the tips . . . . ***Oncosclera***
- Megascleres spiny, stout oxeas; microscleres absent; gemmules present; gemmuloscleres irregularly ovoid strongyles and spiny to smooth oxeas . . . . ***Cherokeesia***